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Survivorship and Predation Changes in Five Populations of *Botrychium dissectum* in Eastern Pennsylvania

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This study of five populations of *Botrychium dissectum* was initiated in 1977 as part of a general environmental monitoring program at the Susquehanna Steam Electric Station. The Botrychium populations were discovered in the course of general flora surveys. Plants of this species were remarkably common in old fields and second growth woodlands on the site; therefore, I decided to monitor these populations in several successional habitats and their fate over several years. Part of the rationale of this study was simply that populations of *Botrychium dissectum* were observed in several plant communities that I could reasonably expect to remain undisturbed at a protected site. The study area is located in the Susquehanna River valley, 8 km north of Berwick, Salem Township, Luzerne County, in east-central Pennsylvania.

Botrychium dissectum produces a single leaf each year from a short underground rhizome. This leaf emerges in mid to late summer, unfolds, and, if a fertile segment is present, spores are shed in early autumn. The fertile segment then withers, but the vegetative blade remains throughout the winter and following spring, senescing as the new leaf emerges. It should be emphasized that if this leaf is damaged or lost, the plant has no photosynthetic organ until the next summer. If the first leaf is damaged as soon as it emerges, occasionally plants will produce a small second leaf.

Although this study was initiated with the idea of following the fate (longevity) and production of fertile fronds of plants in several populations, the study has been "sidetracked" by the discovery that many of the plants were eaten in the autumn soon after the leaf emerged and expanded. The plants have high survival under these conditions; this will be the chief topic of this paper.

METHODS

Individual plants in each population were selected and marked with permanent plastic labels. Since loss of some markers was considered inevitable, a map was prepared of each plant location with nearby trees, rock walls, etc. Plants initially selected for study were fairly separate individuals; that is, clumps of plants where individuals could not be distinguished were avoided. This facilitated relocating plants whose labels were broken or pushed out of the ground.

The study was begun in the spring of 1977 (the leaves would obviously be ones that survived the previous winter). Plants were added in the autumn of 1977 and in 1978 and 1979, especially where there might be confusion if the plants were adjacent to a marked plant. Plants were measured for leaf length, leaf width, the number of segments, and, if fertile, the height of the fertile segment. Measurements were made in spring and autumn 1977 and 1978. After this, the populations were checked in the spring and autumn of each year and leaves were recorded as present, partly eaten, eaten off, or missing, but measurements were made only in autumn. Plants were considered to be present if they were more or less whole and measurements could be made. Eaten off plants were those where a stump was found, indicating that a leaf was produced, but was removed. Missing plants were those where nothing was found except the label.

Measurements and coded information for presence was input on a computer program. Leaf area was calculated from a formula derived from leaf length and width, after determining the area of 86 leaves using the dot planimeter technique suggested by Dolph (1977).

The habitat and plant community associated with each population were measured by surveying the general area of the population with a Brunton compass (to determine area). All trees ($>$ 10 cm dbh) and saplings (1–10 cm dbh) were identified and measured, and percent cover was estimated for trees, shrubs, and herbs. Quadrats 1 m^2 were laid out in a grid to determine the number of *Botrychium dissectum* plants per m^2. All plants including stumps in the quadrat were counted, and mean, minimum, and maximum values were obtained for each population. These measurements were made in October 1979 and May 1988, allowing comparison of values over the ten year period of this investigation.

Results

Interpretation of the basic information on plants present/eaten/missing indicated that the single leaf produced by a plant was often eaten or missing soon after it appeared in late summer. To illustrate what happened in the populations, I prepared a chart for each population showing the fate of each plant at each observation (Fig. 1–5). The population community measurements are summarized in Table 1. Populations 1, 2, and 3 were located in woodlands where the canopy was more or less completely closed and tree diameters and basal area/ha were fairly high. The dominant trees were black oak (*Quercus velutina*) and red maple (*Acer rubrum*). Herbaceous cover was low in both spring and autumn. Population 3 was located in the most mature forest. Populations 1 and 2 were located in younger second growth forests. Populations 4 and 5 were located in abandoned fields where the tree canopy was 0–50% closed and the largest trees or saplings were 24 cm or less in dbh (Table 1). There were scattered trees, saplings, and clumps of shrubs, with open areas dominated by perennials; herbaceous cover was high, especially in the autumn. Population 4 was located in a more mature field where trees had higher percent cover and herbaceous plants lower cover. Population 5 was in a younger field with more open areas dominated by perennials, although after ten years the saplings and shrub clumps were noticeably larger.

TABLE 1. Plant community measurements for five populations of *Botrychium dissectum*. The first number is a 1978 measurement; the second a 1988 measurement, and a single number indicates no change 1978–88.

	Population 1	Population 2	Population 3	Population 4	Population 5
Elevation (m)	177	207	170	192	207
Slope	level	south-facing	west-facing	level	level
Trees: no/ha	476–266	639–501	610–604	200–533	0
Total ba/ha	260693–239710	439167	221304–346520	31856–88083	0
% cover	100–91	100–98	90–80	40–55	0
Largest: dbh	68–71	98	46–73	24–22	(6)
Dominant sp.	*Acer rubrum*	*Quercus velutina*	*Quercus velutina*	*Acer rubrum*	(none)
Associate spp.	*Fraxinus americana* *Prunus serotina*	*Acer rubrum* *Liriodendron tulipifera*	*Acer rubrum* Quercus borealis	*Quercus velutina*	
Saplings: no/ha	750–250	556	1199–854	1042–717	1200
Total ba/ha	12943–5702	9250	17200–12396	24366–17033	13978
Dominant sp.	*Acer rubrum*	*Quercus alba*	*Quercus velutina*	*Acer rubrum*	*Cornus florida*
Shrubs: % cover	64	70	70	16	65
Dominant sp.	*Lindera benzoin*	*Lindera benzoin*	*Rhus radicans*	*Rubus flagellaris*	*Cornus racemosa*
Herbs: % cover-Spr	40	23	1	48	80–60
cover—Autumn	10	< 10	1	80	100–56
Dominant spp.	*Podophyllum peltatum* *Dryopteris intermedia*	*Polystichum acrostichoides*	—	*Solidago* spp. *Fragaria virginiana*	*Solidago canadensis* *Solidago rugosa*
Botrychium plts/m	7.60–1.42	0.43	0.07–0.26	4.91–3.30	3.88–4.33

Abbreviations: ba/ha = basal area per hectare in cm
dbh = diameter breast height in cm
plts/m = number of plants per m

In Population 1 (second growth woods), there were 80 plants (Fig. 1). The number of plants eaten or missing in each autumn ranged from 10–73 (13–91%), with a mean of 22 plants (28%). In spring the number of plants eaten or missing ranged from 22–75 (28–94%), with a mean of 44 plants (55%). In general, except for 1987–88, there were more plants eaten than missing in both autumn and spring. The sudden loss of so many plants in autumn of 1987 was peculiar, in that there was no evident disturbance of the habitat. In this population prior to 1987, 13 plants (16%) have disappeared; all of these are presumed to have died since there were no problems with labels. In autumn 1988, 30 plants (38%) were present in this population, 21 (26%) were eaten, and 29 (36%) were missing. Preliminary data for autumn 1989 indicate a situation more like 1987 (most plants missing). There still is no evident environmental cause for the fluctuations in this population.

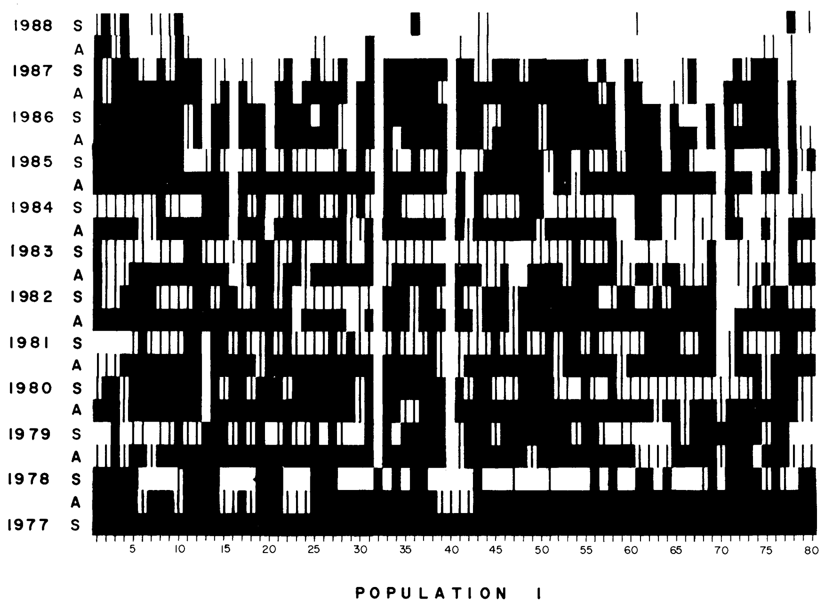

FIG. 1. Status of each plant in Population 1, spring (S) and autumn (A) 1977–88. Each vertical column represents a numbered plant. The condition of the plant at the time of observation is indicated by a solid bar if the plant was present, a line if the plant was eaten off, and blank if the plant was missing.

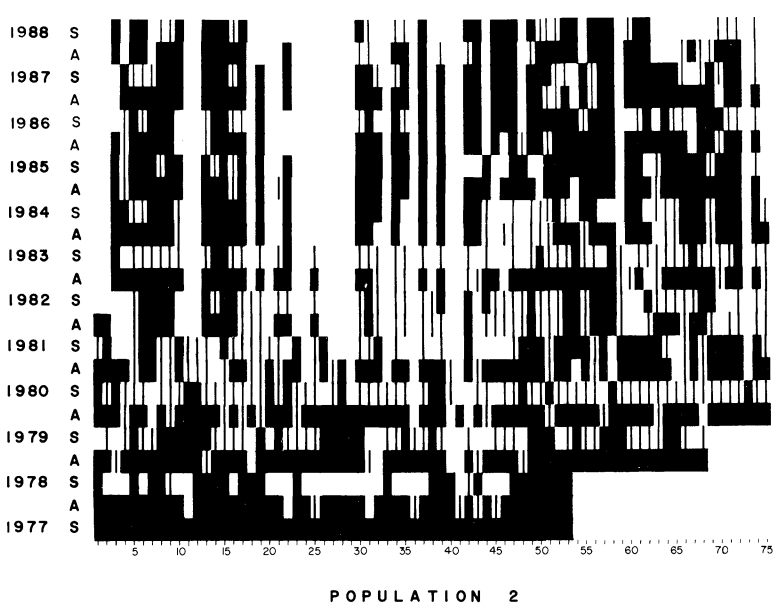

FIG. 2. Status of each plant in Population 2, 1977–88. Explanation same as Fig. 1.

In Population 2 (second growth woods), 53 plants were originally marked, and 22 were added in 1978 and 1979, for a total of 75 (Fig. 2). The number of plants eaten or missing in autumn ranged from 8–49 (15–65%), with a mean of 28 (38%). In spring, the number of plants eaten or missing ranged from 28–66 (53–88%), with a mean of 43 (59%). In this population, 24 plants were permanently missing in 1988, 4 of which were label problems. The remaining 20 plants (27%) have presumably died during the study. Most of these were in a group of plants on a slope, where erosion may have been a problem. Dense shading by shrubs *(Lindera benzoin)* has also occurred in the population, but some plants survived this.

In Population 3 (fairly mature woods), 40 plants were originally marked and 11 were added in 1978–80 (Fig. 3). The number of plants eaten or missing in autumn ranged from 5–23 (12–45%), with a mean of 15 (31%). In spring, the number of plants eaten or missing ranged from 10–28 (25–55%), with a mean of 18 (36%). In this population 8 plants were permanently missing in 1988, 1 because a label was lost and 7 (14%) because of death.

In Population 4 (abandoned field in shrub stage), 62 plants were originally marked, and 38 were added in autumn 1978, for a total of 100 plants (Fig. 4). The number of plants eaten or missing in autumn ranged from 30–70 (30–70%), except in autumn 1978 when 8 of the 65 plants were missing (12%). The mean number was 41 (41%). In spring, the number of plants eaten or missing ranged from 65–92 (65–92%), with a mean of 72. In this population 24 plants were permanently missing by 1988, 12 because of label or plant identification problems, and 12 (12%) were presumably dead. This population had the highest

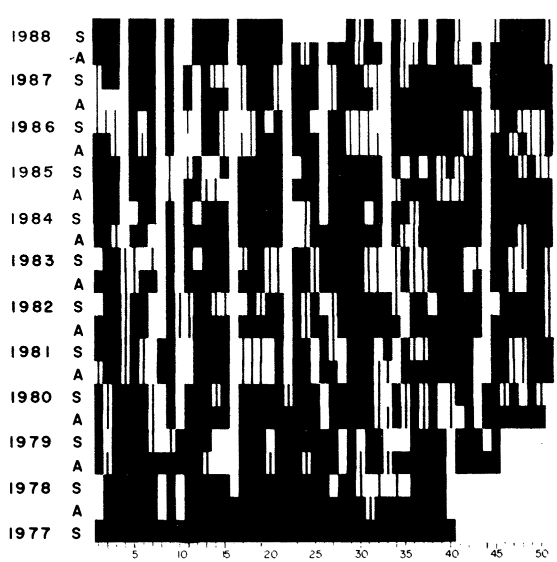

FIG. 3. Status of each plant in Population 3, 1977–88. Explanation same as Fig. 1.

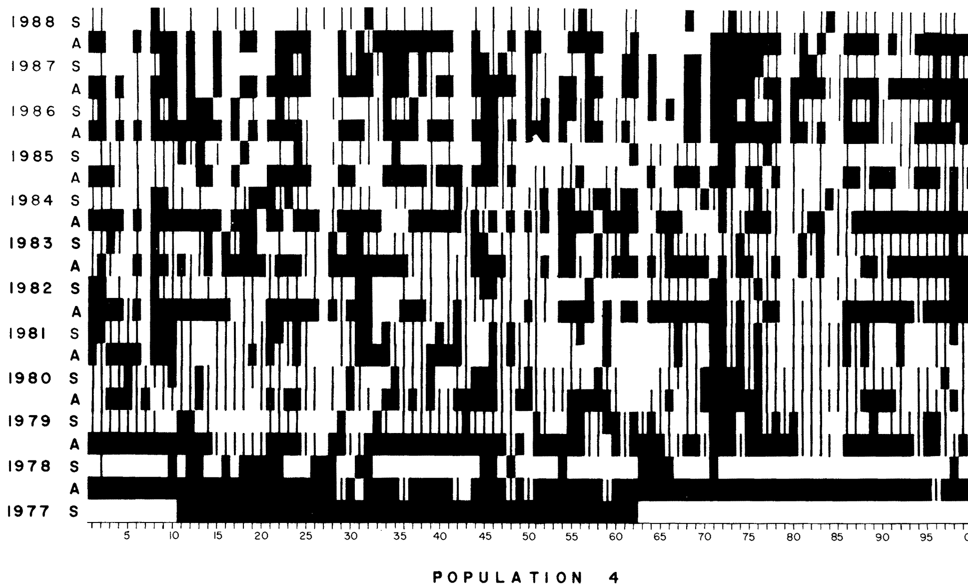

FIG. 4. Status of each plant in Population 4, 1977–88. Explanation same as Fig. 1.

mean percentages of plants eaten or missing by a wide margin (21% in spring and 13% in autumn).

Population 5 (abandoned field) included 64 plants, and 1 was added; studies began in the population in autumn 1978 (Fig. 5) The number of plants eaten or missing in autumn ranged from 11–46 (17–71%), with a mean of 18 (28%). In spring, the number of plants eaten or missing ranged from 26–63 (41–97%), with a mean of 51 (79%). In this population, 7 plants were permanently missing by 1988, 2 because of missing labels and 5 (8%) were dead.

In summary, all populations had 12–91% of the plants eaten or missing in autumn, with means between 28 and 41% (less than half) (Fig. 6). In autumn, the number of plants eaten usually exceeded the number missing. In spring, 25–97% of these plants were eaten or missing, with population means between 36% and 79%. The number missing exceeded the number eaten about one-half the time, especially in more recent years since label problems and mortality are cumulative. The last measurements in spring and autumn 1987/88 did not have the highest percentage of eaten or missing, except in Population 1, where there was a sharp decrease. There was a slight decrease in all populations, as mentioned before, caused by the death or disappearance of plants.

DISCUSSION

It is certainly remarkable that these plants persist. Nearly all of the plants have been eaten at one time or another, and some of them survived this treatment for two or more years. In Population 4 (Fig. 4), ten plants (#4, 6, 37, 38, 41, 84, 88,

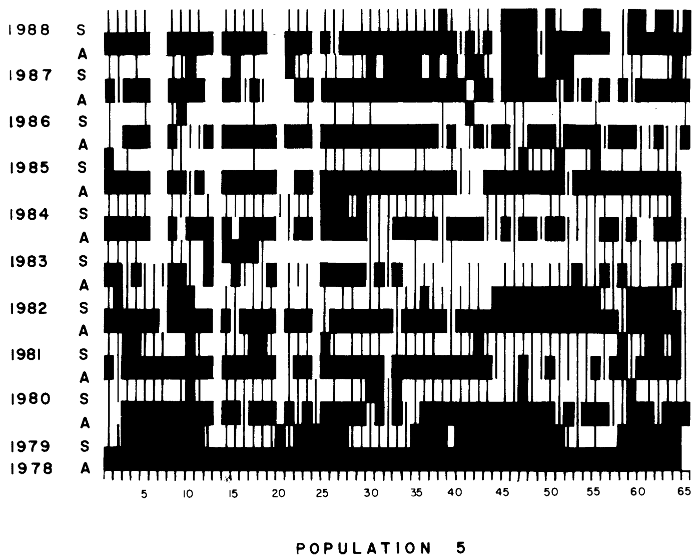

FIG. 5. Status of each plant in Population 5, 1978–88. Explanation same as Fig. 1.

91, 93, 94) were eaten in every spring and yet survived. Thirty plants were eaten for two consecutive autumns; they had photosynthetic organs for less than six weeks for two years at some time during the study. Thirteen plants were eaten for three consecutive years, nine (#15, 17, 51, 73, 80, 81, 82, 83, 85) for four consecutive years; of these, one (#51) was five, one (#80) six, and one (#85) nine years continuously eaten. Although the numbers are not as high in other populations, the pattern is the same: many plants were eaten by spring, year after year, and some were eaten for two or three consecutive years in autumn and continued to survive and produce new leaves in the following year.

Survivorship curves were prepared from data on plants missing for more than two years (Fig. 7). The number of plants surviving, after elimination of label and plant identification problems, was high. Little difference occurred between populations. The number of plants lost ranged from 8–27% of the original total. For all populations combined, 57 plants have disappeared, or 16% of the 352 plants in the five populations. Nineteen plants (5% of the original 371 plants) were eliminated because of label or identification problems.

The survivorship curves indicate that these are long-lived plants. Data on longevity of pteridophytes are sparse. Oinonen (1967a, b) found that individual clones of bracken (*Pteridium aquilinum* (L.) Kuhn.) and ground pine (*Lycopodium complanatum* L.) could be traced for several hundred years. These *Botrychium* plants, which were mature when the study began a dozen years ago, must live at least for several decades.

Several authors have pointed out that herbivores do not often kill the plants on which they feed, except in the seed or seedling stages (Harper, 1977; Dirzo,

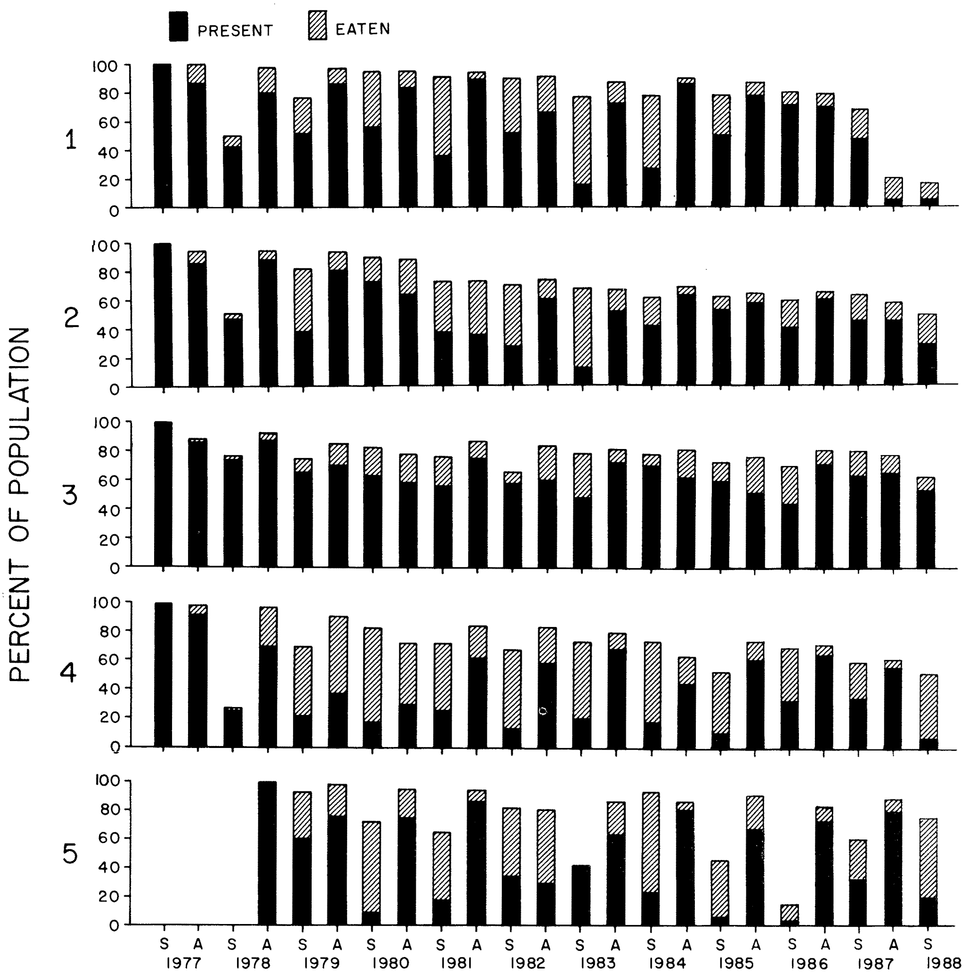

FIG. 6. Percent of plants in each of five *Botrychium dissectum* populations that were present or eaten off, spring (S) and autumn (A) 1977–88.

1984). Even complete defoliation, as of oaks by gypsy moth or cherry by tent caterpillar, is not fatal unless repeated in successive years. Experimental work on flowering plants indicated that removal of up to 75% of the leaves had little effect on survival, unless there were other stresses such as shading (Dirzo, 1984). None of these experiments lasted more than one year, however; all were on tree seedlings with many leaves. The effect of many herbivores on plant populations is to browse on some plants and leave others intact (Harper, 1977), but in this case, where only one leaf is produced, and it is entirely eaten, there is little or no stored food available for the year.

Data from these five populations show that plants can be eaten in the autumn for three or more consecutive years and continue to produce new leaves in

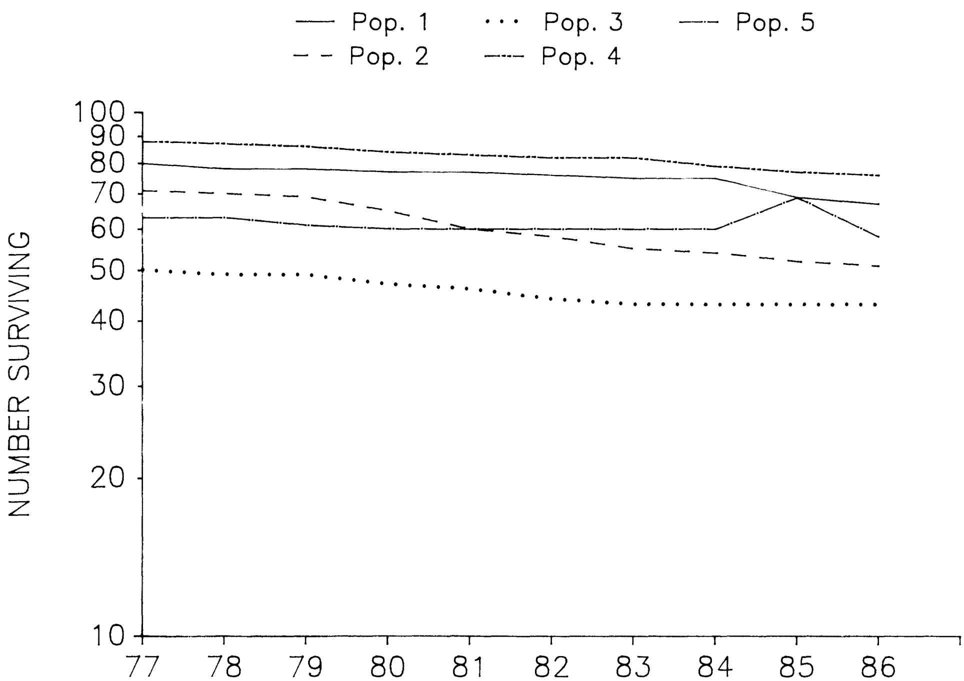

FIG. 7. Number of surviving plants in five populations of *Botrychium dissectum*, 1977–86.

subsequent years. How, then, do these plants continue to survive? The underground bud of the plant contains the leaf primordia for up to five leaves. It is therefore possible that there is enough energy stored in the fleshy rhizome to produce the leaf from the primordium. In a few cases, however, plants have continued to produce leaves for more than five years. Statistical tests, currently under development, will investigate whether the loss of a leaf for two, three, or four years causes a reduction in the size of the leaf or the chances that a plant will produce a fertile leaf.

I would like to suggest another possibility as to how these plants are surviving, based on studies done with orchids. Many terrestrial orchids, like *Botrychium*, have endophytic fungi in the rhizomes. Tamm (1972) reported that mapped plants of the orchids *Dactylorchis incarnata* (L.) Vermln. and *Listera ovata* (L.) R.Br. appeared after a year or two absence. Plants were studied over a 17 year period, and it was not uncommon for an individual to be present in one year and absent in the next. The author attributed this to either snail predation or the orchids not appearing above ground for a year and living off the endophytic fungus. In Great Britain, 463 plants in a population of *Spiranthes spiralis* (L.) Chevall were marked (Wells, 1967). The next year, 123 of these were absent, but the following year, 73 of the 123 reappeared in the population (59%), and 22 of them flowered. Thus *Spiranthes*, like *Botrychium*, is able to pass at least one year as an underground plant. Another orchid, *Cephalanthera rubra*, also with an endophytic fungus in the rhizome, was reported to appear after 20 years of subterranean life (Summerhayes, 1968). The populations of *Botrychium* investigated here behaved like these orchids. They underwent heavy predation soon after the leaf unfolded, so that little energy could be accummulated through photosynthesis. The endophytic fungus in the rhizome must be contributing substantially to the nutrition of these plants for them to survive this treatment.

It is only through long term field studies of natural populations of ferns that we can learn details of their ecology. Fern populations may not have the economic value of commercial timber trees or crop weeds, but they can, as this study demonstrates, lead to a better understanding of the stresses and survival of long-lived herbaceous perennials.

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